THE ROLE OF pH IN STRUCTURING COMMUNITIES OF MAINE WETLAND MACROPHYTES AND CHIRONOMID LARVAE (DIPTERA)

Thomas Woodcock[1], Jerry Longcore[2], Daniel McAuley[2], Terry Mingo[3], Carolyn Reid Bennatti[4], and
Kenneth Stromborg[5]
[1] *Lake Champlain Research Institute*
102 Hudson Hall
Plattsburgh State University
Plattsburgh, New York, USA 12901
E-mail: woodcot@plattsburgh.edu

[2] *U.S. Geological Survey, Biological Resources Division*
Patuxent Wildlife Research Center
5768 South Annex A
Orono, Maine, USA 04469

[3] *Department of Entomology, Deering Hall*
University of Maine
Orono, Maine, USA 04469

[4] *Department of Wildlife Ecology, Nutting Hall*
University of Maine
Orono, Maine, USA 04469

[5] *U.S. Fish and Wildlife Service*
2661 Scott Tower Dr.
New Franken, Wisconsin, USA 54229

Abstract: Aquatic vascular plants, or macrophytes, are an important habitat component for many wetland organisms, and larvae of chironomid midges are ubiquitous components of wetland fauna. Many chironomids are primary consumers of algae and detritus and form an essential energetic link between allochthonous and autochthonous primary production and higher trophic levels, while others are predators and feed on smaller invertebrates. Live macrophytes serve mostly as habitat, whereas plant detritus serves as both habitat and as a food source. Assemblages of macrophytes and chironomid larvae were surveyed in ten Maine wetlands, five with low pH (<5.0) and five with high pH (>5.5), and explained in terms of physical and chemical habitat variables. Macrophyte richness was significantly greater, and richness of chironomid larvae was lower, in low pH wetlands. There was no difference in chironomid abundance related to pH. However, community structure was related to pH, suggesting that competitive dominance of a few taxa was responsible for lower richness in low pH wetlands, whereas competition was weaker in high pH wetlands, making coexistence of more chironomid taxa possible. An examination of individual chironomid taxa by stepwise multiple regression showed that distribution of most taxa was controlled by water chemistry variables and macrophyte habit (i.e., floating, submergent).

Key Words: community structure, water chemistry, wetlands, macrophytes, Chironomidae

INTRODUCTION

Aquatic vascular plants (macrophytes) are an important component of most wetland habitats, and a diverse macrophyte assemblage can increase habitat heterogeneity in a wetland. Sediments covered by macrophytes differ from other wetland habitats in redox potential, light exposure, texture, stability, organic matter content, and variability of temperature and oxygen levels (Sagova et al. 1993). Krecker (1939) hypothesized that macrophytes with finely-dissected leaves should support a greater diversity and biomass of invertebrates because they increase habitat heterogeneity and available surface area for colonization of

both invertebrates and their food resources (biofilm). Finely dissected foliage also may act as a ''sieve'' for seston and plankton (Cyr and Downing 1988, Jeffries 1993). Dvorak and Best (1982) and Jeffries (1993) found evidence that increasing foliar complexity increased abundance (but not necessarily diversity) of colonists, possibly because invertebrate body size was an important determinant of the quantity of usable habitat. In contrast, the research of Gerrish and Bristow (1979) and Cyr and Downing (1988) suggested that the habit of the macrophyte (e.g., floating, submergent, etc.) is more important in structuring the epiphytic invertebrate community. Typically, living macrophytes are considered a physical habitat suitable for periphytic algae, a preferred food resource of aquatic primary consumers (i.e., the ''glass forest''—Rosine 1955, Gerrish and Bristow 1979, Batzer and Wissinger 1996).

Larvae of chironomid midges are ubiquitous components of wetland fauna and are an important component of wetland food webs. Many are primary consumers of algae and detritus and are food for other invertebrates, fish, and waterfowl. They form a crucial link between energetic inputs and higher trophic levels (Schroeder 1973, Batzer and Wissinger 1996, Richardson et al. 1998). Warren and Spencer (1996) determined from their enclosure studies that macrophyte detritus was important as habitat but contributed little to invertebrate energy acquisition, whereas Batzer (1998) reported that quantities of detritus affected availability of both habitat and energy. The dominant taxa (*Chironomus*, *Glyptotendipes*) in these studies, however, do not feed extensively on coarse organic matter, and the response observed by Batzer (1998) occurred mostly after the detritus had broken down into finer particulates. Smock and Stoneburner (1980) documented a switch in food preferences among macrophyte-dwelling invertebrates from periphyton on living plants to decomposing tissue following plant senescence. Various chironomid taxa inhabit sediments with and without macrophytes, and the availability of oxygen is a major determinant of suitability (Sagova et al. 1993, Batzer and Wissinger 1996). Live macrophytes and wood serve mostly as substrate, whereas plant detritus serves as both habitat and as a food source (Smock and Stoneburner 1980, Smock and Harlowe 1983, Warren and Spencer 1996, Batzer 1998, Entrekin et al. 2001). Some chironomids mine in stems of live macrophytes to construct filtering devices for suspended organic matter (Berg 1950, McGaha 1952).

In this paper, we report relationships of macrophyte and chironomid taxa to chemical (pH) and biological habitat features of ten Maine wetlands with different pH values; high (>5.5) versus low (<5.0), which may
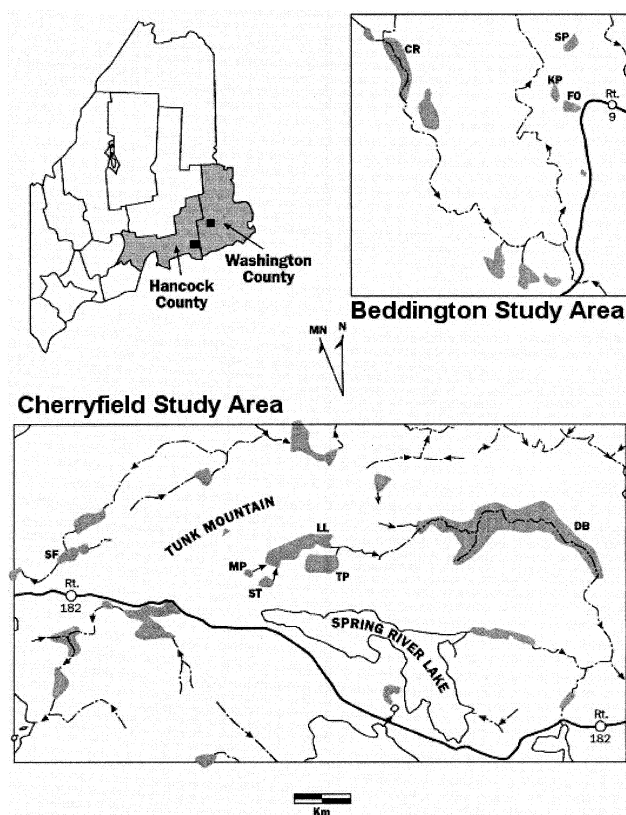

Figure 1. Study areas and locations of individual wetlands in Maine. Crooked River (CR), Fuel Oil Pond (FO), Kerosene Pond (KP), and Salmon Pond (SP) are located in the Beddington study area (Washington County, right inset). Downing Bog (DB), Mud Pond (MP), Little Long Pond (LL), Snake Flowage (SF), Salmon T Pond (ST), and Tilden Pond (TP) are located in the Cherryfield study area (Hancock County, bottom inset).

affect habitat heterogeneity and community characteristics of both macrophytes and invertebrates. Some chironomids are able to tolerate harsh chemical conditions, including low pH (Eilers et al. 1984, Havas and Likens 1984, Yasuno et al. 1985, Berezina 1999). Acid-tolerant chironomids may reach high abundances in low pH wetlands because acid-intolerant insectivorous fish are absent (Batzer and Wissinger 1996).

METHODS

Study Areas

Macrophyte surveys were conducted and chironomid larvae collected from ten wetlands, five wetlands with pH < 5.0 and five wetlands with pH > 5.5 (Figure 1). Three wetlands were beaver-created, and seven were glacial in origin, with no surface connection to flowing water. The Cherryfield study area is located mostly in Township 10 SD, 68° 5′ W Longitude, 44° 40′ N Latitude about 20 km west of Cherryfield,

Maine, USA (1957 U.S.G.S., Tunk Lake Quadrangle, 15-min Series). The Beddington study area is located in the southeast corner of Township 30 MD, 67° 50′ W Longitude, 44° 55′ N Latitude about 13 km east of Beddington, Maine (1941 U.S.G.S. Tug Mountain Quadrangle, 15-min Series). Geomorphological and vegetational characteristics are summarized in Table 1.

Collection and Analysis of Water Samples

Water was sampled in each wetland in early May 1982 and mid-July 1982. Water samples were collected from mid-pond or behind dams of beaver flowages at elbow depth (~35 cm) directly into 500mL polyethylene bottles that had been acid-washed and rinsed in deionized water. In deeper ponds, water samples were obtained from watercraft by lowering a plastic, Van Dorn-type sampler to near bottom at the pond's center. Samples were stored on ice during transport, and analyses for pH, alkalinity, specific conductance, and color were performed within 24h after collecting samples. Glassware and containers were acid-washed in 10% nitric acid and rinsed three times with deionized, glass-distilled water prior to use. Samples were warmed to ambient temperature, and a 100-mL subsample removed for pH and alkalinity measurements. The pH was measured with a portable meter (Fisher Model 640) equipped with a plastic body, gel-filled combination electrode. The electrode was rinsed in deionized water, blotted dry, and placed in the sample for a minimum of 15 minutes. When three successive readings at 1 minute intervals were identical, the pH was recorded. Alkalinity was determined by Gran titration with 0.02N sulfuric acid (Stumm and Morgan 1970). Specific conductance was measured with a Markson Science Inc. Model-10 meter. Color (Hazen units) was determined by comparison of unfiltered samples with a platinum cobalt standard solution (Lamotte Chemical Co., Chestertown, MD).

Anions (F^-, Cl^-, NO_3^-, SO_4^{2-}) were measured with a Dionex Model 16 double channel ion chromatograph, which were compared to external reference and calibration standards. Multiple standards were run sequentially over the course of the seven-hour run. Total reactive phosphorus (P^{3+}) was measured by digestion in 5% potassium persulfate solution then heating at 15 lbs pressure for 0.5h. Standards, blanks, and water samples were read for absorbance in relation to distilled water, with a 10-cm light path cuvette with absorbance at 800 nm measured on a Cary 5 recording spectrophotometer (Wetzel and Likens 1979). Metal cations (Al^{3+}, Ca^{2+}, Mg^{2+}, K^+, Na^+) were measured with a Perkin-Elmer Model 703 Atomic Absorption Spectrophotometer. Na^+ and K^+ cation concentrations were measured with air-acetylene atomic absorption spectrophotometry (AAS), Ca^{2+} and Mg^{2+} were measured by nitrous oxide-acetylene AAS, and Al^{3+} and Mn^{2+} were measured by graphite furnace AAS. Analytical standards were made by combining single metal solutions to yield an artificial water of composition similar to the actual sample.

Macrophyte and Chironomid Sampling and Identification

Samples were collected June 21–28, 1982 at the Cherryfield study area and July 8, 1982 at the Beddington study area. Ten sampling sites were randomly chosen for each wetland by placing a clear, plastic, numbered grid over the wetland map, and selecting ten grids at random. A circular sweep net (cross-sectional area 0.036m², 500-μm mesh size) was used at each sample site to make two 2-m sweeps, one at the water surface and one at the benthic substrate. Macrophytes occurring at each sampling point were identified, together with other benthic habitat types (Filamentous Algae, Flooded Timber, Gravel, Leaf Litter, Moss, Organic Detritus, Sedge/Grass Detritus, Woody Debris). Samples were stored in quart jars and preserved in 70% ethanol. Chironomidae larvae were separated into four major subdivisions (Chironomini, Tanytarsini, Tanypodinae, Orthocladiinae), then further subdivided into groups based on morphology (except for Orthocladiinae). For samples of fewer than ten specimens all specimens were mounted, whereas for samples with many specimens random subsamples were selected. Specimens were slide-mounted in polyvinyl lactophenol to facilitate generic determinations according to Wiederholm (1983).

Data Analyses

Water chemistry, richness of macrophyte taxa, richness of habitat (sum of macrophyte and non-macrophyte habitat types), chironomid richness, equitability (Tokeshi 1992), and Shannon-Weaver Diversity were compared using two-tailed t-tests, grouped by pH level (high vs. low). Significance was accepted for each if $p < 0.05$ (Neter et al. 1996). Because of the semi-quantitative nature of the sampling, a non-parametric Mann-Whitney test (Conover 1980) was used to compare chironomid abundance. Variables were transformed where necessary to meet assumptions of normality and constant variance (Neter et al. 1996).

Rank-ln(Abundance) plots were constructed for chironomids in high and low pH wetlands (Tokeshi 1993), and 95% confidence intervals were constructed for slopes within each group. Canonical Correspondence Analysis (CCA) was performed (Rencher 1995) to relate water chemistry variables (pH, conductivity,

Table 1. Selected physical and biological characteristics for study wetlands in Beddington and Cherryfield, Maine, 1982.

Pond	Class[1]	Origin[2]	Surface Area (ha)	Water Perimeter (m)	Percent Surface Water in Life Forms[3]:					
					Opn	Sub	Flt	Eme	Eri	Fwt
Low pH										
Kerosene Pond	PSSBLE	G	2.62	872	100	24	0	0	0	0
Mud Pond	PUBORG	G	1.60	559	98	16	1	1	0	0
Fuel Oil Pond	PSSBLE	G	0.64	823	0	0	0	92	8	0
Downing Bog	PSSBLE	B	117.1	10936	6	22	20	22	46	6
Salmon Pond	PUBGRA	G	3.96	835	93	1	7	0	0	0
High pH										
Snake Flowage	PFWNLE	B	4.95	1245	10	10	0	28	21	41
Little Long Pond	LRBRUB	G	21.75	2989	99	2	0	1	0	0
Crooked River	PSSBLE	B	5.25	5659	93	93	7	0	0	0
Tilden Pond	LRBRUB	G	12.26	1563	97	0	1	2	0	0
Salmon T Pond	PUBCOB	G	2.45	633	97	3	0	3	0	0

[1] Wetland classification based on Cowardin et al. (1979) P = Palustrine, SS = Scrub shrub, BLE = Broad-leaved evergreen, RB = Rock bottom, ORG = Organic, UB = Unconsolidated bottom, GRA = Gravel, FW = Forested wetland, NLE = Needle-leaved evergreen, L = Lacustrine, RUB = Rubble, COB = Cobble.
[2] B = Beaver, G = Glacial.
[3] Opn = open water, Sub = submerged macrophytes, Flt = floating macrophytes, Eme = emergent vegetation, Eri = Ericaceous vegetation, Fwt = forested wetland.

and concentrations of TOC, alkalinity, cations, total phosphorus, aluminum, sulfate, nitrate, chloride) to vegetation occurrence in each wetland. Vegetation taxa were included if they occurred in three or more ponds, and at five or more stations across all wetlands. An index of coverage for a pond was calculated for each taxon as the number of occurrences (out of ten samples) obtained at a wetland. A second CCA was performed to relate the abundance of chironomid taxa to water chemistry and benthic habitat (macrophyte and non-macrophyte) variables.

RESULTS

In most wetlands, F^{−} and Mn^{2+} were not detectable, so these ions were excluded from further analyses. In the low pH wetlands, mean pH (p=0.0004) and mean alkalinity (p=0.0008) were lower than in the high pH wetlands. Low pH wetlands also had lower mean concentrations of Ca^{2+} (p=0.0005) and Mg^{2+} (p=0.017), and higher concentrations of nitrate (p=0.041) than the high pH wetlands (Table 2). The biological sampling recorded a total of 23 macrophyte and 43 chironomid taxa (Appendix). Macrophyte richness was significantly greater in low pH wetlands, with 2.48 plant taxa recorded per sample site, versus 1.58 per sample in high pH wetlands (Table 3). However, when non-macrophyte habitats were included in the analysis, overall habitat heterogeneity was not different between wetland types. Chironomid abundance and equitability were not different between wetland types, although chironomid richness (5.9 vs. 4.6 taxa per sample) and

Shannon-Weaver diversity (1.31 vs. 1.06) were greater in high pH wetlands.

The rank-abundance plots of all samples summed within each wetland indicate a steeper slope (dominance by fewer taxa) in the low pH wetlands (Figure 2). Comparison of confidence intervals of the mean slopes depicts a marginally significant difference; low pH wetlands had a mean slope of −0.128 (95% C.I. −0.153 to −0.103), high pH wetlands had a mean slope of −0.098 (95% C.I. −0.130 to −0.066). This suggests that the structuring of the chironomid community is influenced by different environmental factors in the two types of wetland.

The distribution of individual taxa in the plant CCA revealed associations with certain wetland types. The first two axes accounted for 23% and 22% of the variability in these data, whereas subsequent axes accounted for little additional variance (<5% each). Three distinct groups of wetlands were evident (Figure 3A) with associated vegetation types (Figure 3B). The first group includes the beaver-created wetlands (Crooked, Downing, Snake) together with the low pH Mud Pond and Fuel Oil Pond. The second group includes the high pH glacial wetlands in the Cherryfield study area (Little Long, Salmon T, Tilden). The third group includes the low pH glacial wetlands in the Beddington study area (Kerosene, Salmon). These groupings suggest that vegetation occurrences are more closely related to geographic location than to habitat characteristics, such as pH, although this effect was less pronounced in the beaver-created wetlands.

The CCA of chironomid response to biotic and abi-

Table 2.   Selected surface water chemistry values for 10 wetlands near Beddington and Cherryfield, Maine, sampled for Chironomidae in July, 1982.

Wetland	pH	Alkalinity (μeq 1^{-1})	Conductivity (μmhos cm^{-1})	Color (Hazen Units)	TOC (mg 1^{-1})	ΣP (μg 1^{-1})
Low pH						
Kerosene Pond	4.48	−37.7	22.5	30	3.159	5.5
Mud Pond	4.71	−20.0	28.0	15	2.239	4.1
Fuel Oil Pond	4.82	−9.3	33.5	130	9.289	18.8
Downing Bog	4.94	−1.2	16.0	60	4.998	32.0
Salmon Pond	5.00	−9.0	15.0	20	2.546	5.3
Mean ± SE	4.79 ± 0.09	−15.4 ± 6.3	23.0 ± 3.5	51 ± 21.2	4.44 ± 1.30	13.4 ± 5.4
High pH						
Snake Flowage	5.51	58.8	24.0	170	11.741	70.0
Little Long Pond	5.90	7.9	24.0	5	1.626	1.6
Crooked River	6.02	45.4	20.5	90	6.837	18.8
Tilden Pond	6.60	37.0	23.5	10	1.933	5.0
Salmon T Pond	6.65	45.9	23.0	10	1.933	4.8
Mean ± SE	6.13 ± 0.22	39.0 ± 8.5	22.9 ± 0.6	57 ± 32	4.84 ± 1.99	20.0 ± 12.8

				(μeq 1^{-1})			
Wetland	Ca^{2+}	Mg^{2+}	K$^+$	Na$^+$	Al^{3+}	SO$_4^{2-}$	NO$_3^-$	Cl$^-$
Low pH								
Kerosene Pond	0.30	10.7	3.6	30.9	1.5	30.4	3.9	35.3
Mud Pond	1.31	24.0	4.9	75.3	29.2	100.0	7.0	66.0
Fuel Oil Pond	1.57	26.0	3.6	166.2	10.4	6.0	1.9	168.0
Downing Bog	1.40	23.1	2.8	43.1	5.9	20.6	2.3	47.1
Salmon Pond	0.82	13.2	4.6	41.3	5.1	39.5	6.8	40.7
Mean ± SE	1.1 ± 0.2	19.4 ± 3.1	3.9 ± 0.4	71.4 ± 24.8	10.4 ± 3.1	39.3 ± 16.2	4.4 ± 1.1	71.4 ± 24.7
High pH								
Snake Flowage	2.97	43.0	15.6	83.1	13.2	6.0	3.0	61.0
Little Long Pond	2.15	29.7	6.1	87.4	4.1	82.0	0.0	86.0
Crooked River	2.57	26.4	10.5	89.2	18.1	30.6	0.0	93.0
Tilden Pond	2.64	29.7	5.6	86.1	1.6	58.0	3.0	77.0
Salmon T Pond	2.94	31.4	6.4	80.5	0.0	53.0	0.0	74.0
Mean ± SE	2.7 ± 0.1	32.0 ± 2.9	8.8 ± 1.9	85.3 ± 1.5	7.4 ± 3.5	45.9 ± 12.9	1.2 ± 0.7	78.2 ± 5.4

[1] Color (Hazen units) was converted to total organic carbon (TOC) by the regression, TOC (mg 1^{-1}) = 1.32 + 0.0613 × Color (Haines and Akielaszek, 1983).

otic habitat factors was inconclusive, with no axis accounting for more than 7% of the variance in these data. The presence or absence of most chironomid taxa was much less strongly related to the presence of individual plant taxa than to chemical habitat variables.

Live macrophytes, as a habitat type, had an associated chironomid fauna. Water chemistry variables, however, were the most important determinant of chironomid assemblages, followed by broader categories of benthic habitat types (Filamentous Algae, Flooded Tim-

Table 3.   Summary of pH-related differences in macrophyte and chironomid larvae assemblage descriptors. p-values are given for simple t-tests, with the exception of chironomid abundance, which was a non-parametric (Mann-Whitney U) comparison.

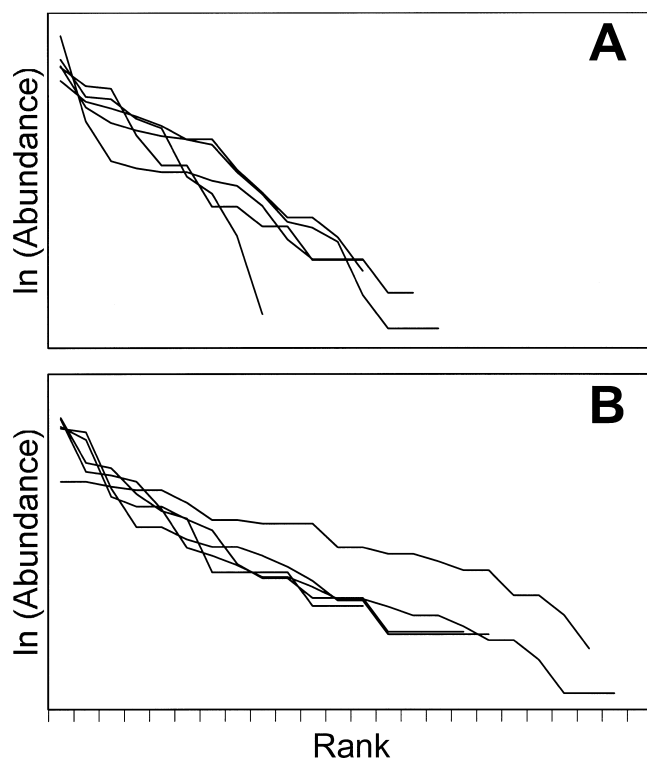|	Metric	Difference	p-value
Habitat	● richness	—	0.052
Macrophyte	● richness	high pH < low pH	0.001
Chironomid	● richness	high pH > low pH	0.019
	● equitability	—	0.364
	● Shannon-Weaver diversity	high pH > low pH	0.020
	● abundance	—	0.469

Figure 2. Rank-ln(Abundance) plots for the ten study ponds, categorized as low pH (A, pH<5.0) and high pH (B, pH>5.5).

ber, Leaf Litter, Moss, Organic Detritus, Sedge/Grass Detritus, Woody Debris). Similarly, no pattern in pond origin or pH was evident, except that of the high pH glacial wetlands. Thus, individual stepwise multiple regressions (Rencher 1995, Neter et al. 1996) were performed to determine habitat preferences for each chironomid taxon that occurred in ten or more samples. Several chironomid taxa (i.e., *Ablabesmyia* sp. 3, *Procladius* (*Holotanypus*), *Dicrotendipes*) showed a habitat preference for living macrophytes, and sometimes a preference for a certain type(s) of macrophyte (Table 4). Most taxa evidently prefer various sorts of detritus as benthic habitat, but in most instances, one or more chemical habitat variables also determined the niche. Only four taxa showed a preference for a certain pH condition; *Paratanytarsus*, *Procladius* (*Psilotanypus*), and the *Thienemannimyia* group preferred high pH, and *Tanytarsus* showed a slight preference for low pH wetlands.

DISCUSSION

The chemical characteristics of the wetlands in this study indicated effects of both geographic location and pH. Glacial ponds formed two separate groups, which may have been related either to pH or to geography. The high pH glacial ponds (Little Long, Salmon T,

Tilden) formed a single group, as did two (Fuel Oil, Mud) of the three low pH glacial ponds. This suggests that vegetational characteristics, including richness (Table 3) may have been more affected by geographic location than pH. The grouping of the three beaver flowages (Downing, Crooked, Snake), however, suggests little effect of pH or geographic location in this type of wetland, and the tendency of beaver-created wetlands to be more similar to each other than those of glacial origin.

The vegetation grouped roughly into three assemblages (Figure 3B). Many macrophyte taxa were biased toward beaver-created wetlands, regardless of pH. Some plant taxa, however, have a distinct preference for glacial ponds, be they low pH (*Eriocaulon*) or high pH (*Nymphaea*, *Isoetes*). This is consistent with the role of beaver as ''ecosystem engineers;'' their activities can have a profound effect on many habitat characteristics (Lawton and Jones 1995, Collen and Gibson 2001). Ray et al. (2001) found that beaver activity increases macrophyte richness in comparison to other lotic systems, with peak diversity occurring in ponds 11–40 years old. In this study, low pH also was associated with higher macrophyte richness (Table 3), although the CCA results indicate that actual macrophyte species present were dissimilar between the two pH levels (Figure 3). Overlap in the assemblages was mostly restricted to beaver-created wetlands, suggesting that pH was not a factor that excluded some species in the presence of beaver. Beaver activity may allow coexistence of more species by acting as a disturbance and not allowing dominance of certain species.

The distributions and assemblage structure of chironomid larvae were controlled more strongly by water chemistry and broader habitat categories (i.e., macrophyte vs. non-macrophyte) than by the plant species present (Figure 2, Table 4). Larvae of many chironomid taxa are capable of tolerating a broad range of water chemistry conditions, in part because they have ion regulatory structures (anal papillae). Pupae have no such structures, and, thus are often the most susceptible life stage to hydrochemical environmental filters. Berezina (1999) documented pupal susceptibility to chemical stress with *Omisus caledonicus* (Edwards), which had larvae tolerant of a broad range of conditions but required a narrower window for successful adult emergence. In this study, pH alone did not affect chironomid abundance but did have an effect on how the community was structured (Figure 2). Although the community structure categories of Tokeshi (1993) are not rigidly defined, a low pH system seems to encourage dominance by fewer species (''Dominance Preemption'' model). Conversely, high pH wetlands are closer to the ''Random Assortment'' model, where

Figure 3. Results of CCA ordination of wetland vegetation, showing axis scores of wetlands and termini of descriptive vectors (A) and associated distribution of vegetation taxa (B). Low pH wetlands are highlighted in black. *Rhododendron canadense* (L.) is presented by a common name, Rhodora.

Table 4. Habitat preferences of common wetland chironomid taxa (minimum 10 occurrences, total occurrences shown in parentheses), as determined by multiple regression analysis. Variables are ordered according to the strength of their influence (positive or negative) on that taxon. Macrophyte preference is expressed when plants are grouped by function.

Taxon	Positive Factors	Negative Factors	Model r^2	Chironomid Macrophyte Preference
Ablabesmyia sp. 1 (40)	[phosphorus], [sulfate], *Andromeda, Brasenia, Sparganium*	[nitrate], *Isoetes*, leaf litter	0.51	floating
Ablabesmyia sp. 2 (29)	[Mg^{2+}], [K$^+$], [nitrate], *Elatine, Lysimachia*	[Ca^{2+}], [aluminum], *Rhododendron canadense* (L.), flooded timber, moss, sedge/grass detritus	0.68	—
Ablabesmyia sp. 3 (25)	*Calamagrostis, Carex*, organic detritus	conductivity, [K$^+$], moss	0.50	emergent grass
Ablabesmyia sp. 4 (14)	alkalinity, *Eleocharis*, flooded timber	[K$^+$], *Isoetes*	0.31	—
Chironomus (26)	moss, sedge/grass detritus, *Carex*, flooded timber	*Calamagrostis*, [DOC]	0.54	—
Dicrotendipes (34)	*Pontederia, Sparganium, Isoetes*	*Nymphaea, Utricularia, Eriocaulon*	0.32	emergent herbs
Paratanytarsus (10)	high pH, [nitrate], *Pontederia, Potamogeton*	[Cl$^-$], *Eriocaulon, Nymphaea, Utricularia*, woody debris	0.55	emergent herbs
Polypedilum (33)	sedge/grass and organic detritus, [phosphorus]	[Na$^+$], alkalinity	0.63	—
Procladius (Holotanypus) (31)	*Andromeda*, [aluminum], *Brasenia, Potamogeton, Myrica, Glyceria*	conductivity, *Chamaedaphne*	0.48	floating, creeping submergent
P. (Psilotanypus) (17)	high pH	leaf litter	0.14	—
Psectrocladius s. str. (37)	*Vaccinium, Nuphar*	—	0.37	floating, emergent shrub
P. (Allopsectrocladius) (13)	filamentous algae, *Glyceria*, flooded timber	*Lysimachia*, leaf litter, *Eleocharis*	0.57	emergent shrub
P. (Monopsectrocladius) (19)	[aluminum], organic detritus	[DOC], *Rhododendron canadense* (L.)	0.48	—
Tanytarsus (35)	organic detritus, [sulfate], low pH	—	0.38	—
Thienemannimyia group (10)	*Andromeda*, high pH	—	0.24	—

comparatively moderate habitat conditions together with random disturbances enable coexistence of a larger number of species. This suggests that high pH wetland assemblages are structured by weak competition and stochastic patch dynamics (Tokeshi and Townsend 1987).

As a general ecological rule, greater habitat heterogeneity leads to greater diversity because of the availability of more niches for colonizers, although in this study, the greater richness of vegetation in low pH wetlands did not translate into increased chironomid richness. Evidence exists that habitat partitioning does occur among chironomids on macrophytes but is weak and occurs within plants rather than between species of plants. Partitioning may represent a result of competition, or avoidance of competition among individuals, but is difficult to document because spatial and

nutritional resources tend to be somewhat homogenous on macrophyte surfaces (Drake 1983, Tokeshi and Townsend 1987). The presence of plant secondary compounds and suitability of the plant surface for algal colonization also are likely important (Dvorak 1987). Decomposition may improve nutritional value of the macrophyte tissue and decrease allelopathic secondary compounds (Smock and Stoneburner 1980). Grass and sedge detritus is nutritionally superior to wood and leaves (Entrekin et al. 2001), but differences are likely to decrease with the length of the conditioning period. This could explain why the various detrital habitats seem to be equally as important as are macrophytes in general when discussing habitat heterogeneity in these wetlands.

The addition of a low pH environmental filter to a situation where stochastic patch dynamics allows co-

existence of a larger assemblage in which no taxon (or group of taxa) are able to achieve dominance (Tokeshi and Townsend 1987) may give a competitive advantage to a few tolerant taxa. Tokeshi (1992) found that similar ''stochastically dynamic'' conditions allowed a community to remain relatively constant when affected by a weak, random disturbance. Furthermore, empirical evidence herein suggests that the nature of chironomid assemblage structures can be affected on a fundamental level by pH, an important concept when acid deposition is an ongoing concern in northeastern North America (Raddum 1980, McNicol 1999, 2002, Doka et al. 2003, Jeffries et al. 2003). Activities of beaver may play a similar role in the structuring of macrophyte communities, which is a potential area for future research.

ACKNOWLEDGMENTS

LITERATURE CITED

Batzer, D. P. 1998. Trophic interactions among detritus, benthic midges, and predatory fish in a freshwater marsh. Ecology 79:1688–1698.

Batzer, D. P. and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. Annual Review of Entomology 41:75–100.

Berezina, N. A. 1999. Tolerance of *Omisus caledonicus* (Diptera: Chironomidae) to changes in salinity, pH, and ionic composition of water. Russian Journal of Ecology 30:58–60.

Berg, C. O. 1950. Biology of certain Chironomidae reared from *Potamogeton*. Ecological Monographs 20:84–101.

Collen, P. and R. J. Gibson. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish—a review. Reviews in Fish Biology and Fisheries 10:439–461.

Conover, W. J. 1980. Practical Nonparametric Statistics, 2nd edition. John Wiley & Sons, New York, NY, USA.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Washington DC, USA.

Cyr, H. and J. A. Downing. 1988. The abundance of phytophilous invertebrates on different species of submerged macrophytes. Freshwater Biology 20:365–374.

Doka, S. E., D. K. McNicol, M. L. Mallory, I. Wong, C. K. Minns, and N. D. Yan. 2003. Assessing potential for recovery of biotic richness and indicator species due to changes in acidic deposition and lake pH in five areas of southeastern Canada. Environmental Monitoring and Assessment 88:53–101.

Drake, C. M. 1983. Spatial distribution of chironomid larvae (Diptera) on leaves of the bulrush in a chalk stream. Journal of Animal Ecology 52:421–437.

Dvorak, J. 1987. Production-ecological relationships between aquatic vascular plants and invertebrates in shallow waters and wetlands—a review. Archiv für Hydrobiologie—Ergebnisse der Limnologie 27:181–184.

Dvorak, J. and E. P. H. Best. 1982. Macro-invertebrate communities associated with macrophytes of Lake Vechten: structural and functional relationships. Hydrobiologia 95:115–126.

Eilers, J. M., G. J. Lien, and R. G. Berg. 1984. Aquatic organisms in acidic environments: a literature review. Technical Bulletin 150, Wisconsin Department of Natural Resources, Madison, WI, USA.

Entrekin, S. A., S. W. Golladay, and D. P. Batzer. 2001. The influence of plant community on chironomid secondary production in two wetland types: cypress-gum swamps and grass-sedge marshes. Archiv für Hydrobiologie 152:369–394.

Gerrish, N. and J. M. Bristow. 1979. Macroinvertebrate associations with aquatic macrophytes and artificial substrates. Journal of Great Lakes Research 5:69–72.

Haines, T. A. and J. Akielaszek. 1983. A regional survey of chemistry of headwater lakes and streams in New England: vulnerability to acidification. U.S. Fish and Wildlife Service, Eastern Energy and Land Use Team, Washington, DC, USA. FWS/OBS-80/40.15.

Havas, M. and G. E. Likens. 1984. Toxicity of aluminum and hydrogen ions to *Daphnia catawba*, *Holopedium gibberum*, *Chaoborus punctipennis*, and *Chironomus anthrocinus* from Mirrow Lake, New Hampshire. Canadian Journal of Zoology 63:1114–1119.

Jeffries, D. S., T. A. Clair, S. Couture, P. J. Dillon, J. Dupont, W. Keller, D. K. McNicol, M. A. Turner, R. Vet, and R. Weeber. 2003. Assessing the recovery of lakes in southeastern Canada from the effects of acidic deposition. Ambio 32:176–182.

Jeffries, M. 1993. Invertebrate colonization of artificial pondweeds of differing fractal dimension. Oikos 67:142–148.

Krecker, F. H. 1939. A comparative study of the annual population of certain submerged plants. Ecology 20:553–562.

Lawton, J. H. and C. G. Jones. 1995. Linking species and ecosystems: Organisms as ecosystem engineers. p. 141–150. *In* C.G. Jones and J.H. Lawton (eds.) Linking Species and Ecosystems. Chapman and Hill, New York, NY, USA.

McGaha, Y. J. 1952. The limnological relations of insects to certain aquatic flowering plants. Transactions of the American Microscopical Society 71:355–381.

McNicol, D. K. 1999. The Canadian Wildlife Service Acid Rain Biomonitoring Program-Monitoring and modelling the effects of acid rain on waterbirds in eastern Canada. p. 80–88. *In* G. G. Raddum, B. O. Rosseland, and J. Bowman (eds.) Proceedings of a Workshop on Biological Assessment and Monitoring: Evaluation and Models, Zakopane, Poland. ICP Water Report 50, Norwegian Institute for Water Research, Oslo, Norway.

McNicol, D. K. 2002. Relation of lake acidification and recovery to fish, common loon and common merganser occurrence in Algoma Lakes. Water, Air and Soil Pollution: Focus 2:151–168.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied Linear Statistical Models, 4th edition. Richard D. Irwin Inc., Boston, MA, USA.

Raddum, G. G. 1980. Comparison of benthic invertebrates in lakes with different acidity. p. 330–331. *In* D. Drablos and A. Tollan (eds.) Ecological Impact of Acid Precipitation. Proceedings of an International Conference, SNSF Project, Sandefjord, Norway.

Ray, A. M., A. J. Rebertus, and H. L. Ray. 2001. Macrophyte succession in Minnesota beaver ponds. Canadian Journal of Botany 79:487–499.

Rencher, A. C. 1995. Methods of Multivariate Analysis. John Wiley & Sons, New York, NY, USA.

Richardson, W. B., S. J. Ziegler, and M. R. Dewey. 1998. Bioenergetic relations in submerged aquatic vegetation: an experimental

test of prey use by juvenile bluegills. Ecology of Freshwater Fish 7:1–12.

Rosine, W. N. 1955. The distribution of invertebrates on submerged aquatic plant surfaces in Muskee Lake, Colorado. Ecology 36: 308–314.

Sagova, M., M. S. Adams, and M. G. Butler. 1993. Relationship between plant roots and benthic animals in three sediment types of a dimictic mesotrophic lake. Archiv für Hydrobiologie 128: 423–436.

Schroeder, L. D. 1973. A literature review on the role of invertebrates in waterfowl management. Wildlife Research Section and Cooperative Wildlife Research Unit, Colorado Division of Wildlife, Denver, CO, USA. Special Report No. 29.

Smock, L. A. and D. L. Stoneburner. 1980. The response of macroinvertebrates to aquatic macrophyte decomposition. Oikos 35: 397–403.

Smock, L. A. and K. L. Harlowe. 1983. Utilization and processing of freshwater wetland macrophytes by the detritivore *Asellus forbesi*. Ecology 64:1556–1565.

Stumm, W. and J. J. Morgan. 1970. Aquatic Chemistry. Wiley Interscience, New York, NY, USA.

Tokeshi, M. 1992. The structure of diversity in an epiphytic chironomid community. Netherlands Journal of Aquatic Ecology 26: 461–470.

Tokeshi, M. 1993. Species abundance patterns and community structure. Advances in Ecological Research 24:111–186.

Tokeshi, M. and C. R. Townsend. 1987. Random patch formation and weak competition: coexistence in an epiphytic chironomid community. Journal of Animal Ecology 56:833–845.

Warren, P. H. and M. Spencer. 1996. Community and food-web responses to the manipulation of energy input and disturbance in small ponds. Oikos 75:407–418.

Wetzel, R. G. and G. E. Likens. 1979. Limnological Analyses. W.B. Saunders Publishing Company, Philadelphia, PA, USA.

Wiederholm, T. (ed.). 1983. Chironomidae of the Holarctic region—keys and diagnoses part I larvae. Entomologica Scandinavica suppl. 19.

Yasuno, M., S. Hatakeyama, and Y. Sugaya. 1985. Characteristic distribution of chironomids in the rivers polluted with heavy metals. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:2371–2377.

Appendix. Summary of larval chironomid occurences, summarized by pH and wetland. Location codes are according to the map (Figure 1).

	Low pH					High pH				
	DB	FO	KP	MP	SP	CR	LL	ST	SF	TP
Tanypodinae										
Ablabesmyia sp. 1	X		X	X		X	X	X	X	X
Ablabesmyia sp. 2	X	X	X	X			X	X	X	X
Ablabesmyia sp. 3	X		X		X	X		X	X	X
Ablabesmyia sp. 4	X					X		X	X	
Apsectrotanypus					X			X		
Clinotanypus					X			X		
Labrundinia	X		X							
Larsia							X		X	
Macropelopia					X					
Pentaneura						X				
Procladius (Psilotanypus)	X	X			X	X		X	X	X
Procladius (Holotanypus)	X	X	X	X	X	X		X	X	
Psectrotanypus	X	X					X		X	
Tanypus						X				
Thienemannimyia group						X	X	X	X	
Orthocladiinae										
Cricotopus	X		X				X		X	X
Eukiefferiella								X		
Nanocladius						X				
Psectrocladius (s. str.)	X	X	X	X	X	X	X	X	X	X
P. Allopsectrocladius)		X				X			X	
P. (Monopsectrocladius)		X	X	X	X	X			X	X
Thienemanniella							X			
Chironomini										
Chironomus	X	X	X	X		X	X	X	X	
Cryptochironomus										X
Cryptotendipes					X					
Dicrotendipes	X	X	X	X		X	X	X	X	X
Einfeldia									X	
Endochironomus									X	
Glyptotendipes			X		X		X			
Harnischia						X	X	X		
Kiefferulus									X	
Lauterborniella								X		
Microchironomus		X						X		X
Microtendipes	X		X			X	X	X		
Parachironomus		X							X	
Paratendipes		X								
Polypedilum	X	X	X	X	X		X	X	X	
Pseudochironomus					X		X	X		X
Stenochironomus			X				X			X
Stictochironomus	X								X	
Tanytarsini										
Cladotanytarsus							X	X		
Paratanytarsus								X	X	X
Tanytarsus	X		X	X	X	X	X	X	X	